A reassessment of the species of *Truncatellina* (Gastropoda: Vertiginidae) in the Iberian Peninsula and North-west Africa

Revisión de las especies de *Truncatellina* (Gastropoda: Vertiginidae) en la Península Ibérica y NO de África

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ABSTRACT

Taxonomy and distribution are reviewed for the tiny land snails of the genus *Truncatellina*, mainly in SW. France, the Iberian Peninsula and NW. Africa (Morocco and Algeria). *T. beckmanni* Quintana, 2010 was recently named as an endemic of Menorca (Balearic Islands). The same distinctive but rather variable species occurs in Portugal and Andalucia. *T. callicratis* is shown to be the commonest and most widespread species in Iberia and NW. Africa. Its southern populations in the Algarve, Andalucia, Morocco and Algeria mainly consist of shells lacking apertural teeth, whereas those in most populations further north have three small teeth. The sequence of development of apertural teeth in this species is discussed in detail. Shells of coexisting *T. callicratis* with and without teeth do not differ in other characters and partial development of teeth is common in many populations, so they are all regarded as conspecific. On this basis, several taxa with the apertural teeth reduced or lacking are treated as synonyms of *T. callicratis*, from England, Croatia, Greece, Algeria, Tunisia and Libya. Those Iberian and NW. African shells lacking teeth have hitherto often been misidentified as *T. cylindrica*, but this appears to be a predominantly northern species (recorded south to the French Pyrenees) differing in other shell characters. *T. arcyensis* Klemm, 1943 intergrades with *T. cylindrica* and is therefore treated as a synonym of that species. An identification key to the W. European and NW. African species is presented, based on characters of adult shells.

RESUMEN

Se revisan la taxonomía y distribución de los pequeños caracoles del género *Truncatellina*, principalmente del SO de Francia, la Península Ibérica y el NO de África (Marruecos y Argelia). *T. beckmanni* Quintana, 2010 fue recientemente descrita como un endemismo de Menorca (Islas Baleares). La misma característica, aunque bastante variable especie está presente también en Portugal y Andalucía. *T. callicratis* ha resultado ser la especie más común y de más amplia distribución en Iberia y NO de África. Sus poblaciones más meridionales, en el Algarve, Andalucía, Marruecos y Argelia, consisten principalmente en conchas con la abertura desprovista de dientes, mientras que la mayoría de las poblaciones que viven más al norte tienen tres pequeños dientes. La secuencia del desarrollo de los dientes de la abertura en esta especie se discute en detalle. La conchas de *T. callicratis* con o sin dientes que coexisten, no se distinguen por otros caracteres y el desarrollo parcial de dientes en común en muchas poblaciones, por lo que todas ellas son consideradas como conespecíficas. Sobre esta base, numerosos táxones de Inglaterra, Croacia, Grecia, Argelia, Túnez y Libia con los

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dientes aperturales reducidos o ausentes son considerados sinónimos de *T. callicratis*. Las conchas ibéricas y del NO de África sin dientes han sido a menudo clasificadas como *T. cylindrica*, aunque ésta resulta ser una especie predominantemente del norte, que se distribuye hacia el sur hasta los Pirineos franceses y que difiere en otros caracteres de la concha. *T. arcyensis* Klemm, 1943 está solapada con *T. cylindrica*, por lo que se considera sinónimo de esta especie. Se presenta una clave de identificación de las especies de Europa occidental y NO de África, basada en caracteres de conchas adultas.

INTRODUCTION

The genus *Truncatellina* comprises numerous species of tiny land snails that occur in the Palearctic and Afrotropical Regions with a few in the Indo-Malayan region. The only comprehensive review was by Pilsbry (1920-1921), which brought some order to usage of names from what he termed the "semi-mythical" period (1774-1821) and provided a detailed monograph of all the taxa then known. Seventeen additional species have been named in the past ninety years, from Europe (Klemm, 1943; Štamol, 1995; Triantis, Pokryszko, Vardinoyannis and Mylonas, 2004; Quintana, 2010), Macaronesia (Hutterer and Groh, 1991), N. Africa (Zilch, 1962), tropical Africa (e.g. Van Bruggen, 1994) and Asia (e.g. Pokryszko, Auffenberg, Hlavac and Naggs, 2009).

In north-western and central Europe the taxonomy of the genus now seems to mostly be well understood and stable (cf. Kerney and Cameron, 1979; Falkner, Bank and von Proschwitz, 2001; Falkner, Ripken and Falkner, 2002; Fauna Europaea Database Project, 2011). Recent published accounts for the Iberian Peninsula mainly report two species that are widespread in Europe, *T. callicratis* (Scacchi, 1833) and *T. cylindrica* (A. Férussac, 1807). These are mapped as about equally common in N. Spain (Altonaga, Gómez, Martín, Prieto, Puente and Rallo, 1994), both are shown as widespread in Andalucia (Ruiz, Cárcaba, Porras and Arrébola, 2006) and both are listed as occurring in Catalonia (Bech, 1990) and the Comunidad Valenciana (Martínez-Ortí and Robles, 2003). For Portugal, Nobre (1941: 152-153) reported only *T. cylindrica* (as *Vertigo muscorum* (Draparnaud)), at numerous localities from Trás-os-Montes to the Algarve. In addition, *T. claustralis* (Gredler, 1856) is reported from Albacete Province and the Comunidad Valenciana (Martínez-Ortí and Robles, 2003: 84-85) and perhaps Catalonia (Bech, 1990), *T. doumeti* Letourneux and Bourguignat, 1887 from near Barcelona (Altimira, 1969, cited by Bech, 1990) and *T. beckmanni* has recently been named from Menorca where it was regarded as an endemic (Quintana, 2010). There is very little modern information published on *Truncatellina* in NW. Africa, from where old reports summarised by Pilsbry (1920-1921) refer to *T. cylindrica* (Morocco, Algeria and Tunisia), *T. doumeti* (type-locality in Tunisia) and *T. callicratis* [as *T. rivierana* (Benson, 1854)] (in Algeria).

In our material from Spain, Portugal, Morocco and Algeria *T. callicratis* is the only common species, with no definite *T. cylindrica* from anywhere south of the French side of the Pyrenees. It appears that the common Iberian and NW. African forms of *T. callicratis* lacking teeth in the shell aperture have been widely misidentified as *T. cylindrica*. The only other species we found was *T. beckmanni*, with specimens from C. and S. Portugal and Andalucia. This taxon varies considerably in size, with small specimens from Portugal exactly matching topotypical *T. beckmanni* from Menorca. We provide data on the shell characters of *T. beckmanni*, *T. callicratis* and *T. cylindrica* and discuss their taxonomy. An identification key to the W. European and NW. African species is also presented, based on characters of adult shells.

PILSBRY (1920-1921) used an essentially typological species concept applied to shell specimens and some subsequent studies have used similar methods. However, KENNARD AND WOODWARD (1923) paid more attention to variability in shell characters in reviewing the British species and some recent studies such as that by QUINTANA (2010) have considered character variation in detail. The scanty information available on genital anatomy of the genus (WATSON, 1923; STEENBERG, 1925; POKRYSZKO, 1990), discloses very simple distal genitalia that seem unlikely to provide useful taxonomic characters. In the absence as yet of data from molecular genetics, it would appear that the best current approaches to judging species-limits in the genus may consist in studying variability of shell characters within and between populations, along with any evidence of sympatric occurrence of taxa.

MATERIAL AND METHODS

Field collections by the authors were made by direct searching, usually accompanied by sieving plant debris and surface soil using nested 2.0 and 0.5 mm mesh sieves. The resulting "fines" were then usually searched at low magnifications using a stereo-microscope. All shells found were retained to avoid possible bias in favour of large or well preserved specimens. Attempts were made to collect population samples with numerous shells from as many sites as possible. Prior to 2001 localities were judged from vehicle mileage readings in conjunction with road maps at 1:200,000 to 1:350,000 scales and altitudes were mainly measured using a barometric altimeter. From 2007 onwards most localities and altitudes recorded by DTH and GAH were obtained using a hand-held Garmin GPS accurate to within 10 metres. Habitat notes (including bedrock type and vegetation) and associated Mollusca were recorded at almost all of the sites.

Shells of adults were distinguished from those of immatures by possession of a markedly expanded and somewhat thickened edge to the peristome. Only adult shells were used for shell measurements and descriptions of apertural teeth. Occasional individual shells that had grown very high without developing a reflected or thickened peristome were not used.

The literature often refers to the teeth as denticles when they are small, or folds when they are large and elongate, but all such protuberances are termed teeth in this account. A shorthand notation was used in scoring teeth of individual shells, taking the names in alphabetical order as columellar, palatal, parietal; thus *e.g.*, 111= all three teeth present, 000= no teeth present, 101= columellar and parietal present but not palatal. Shells were not scored for presence or absence of teeth unless the normal locations of all three teeth were clear of dirt, soil or detritus so they could be seen clearly through the shell mouth. Presence of a palatal tooth was not scored by looking at the back of the mouth, since a very small tooth would often be invisible through the shell wall. Studies of apertural teeth were made using a Meiji RZ series stereomicroscope, intense illumination from a Schott KL 1500 light source via twin fibre-optic swan necks, and tilting or rotating the shells using a very fine, damp paintbrush.

Shell height was measured as the maximum from the top of the protoconch to the lowest part of the outer basal edge of the peristome; shell breadth as the maximum width of the spire, with the shell aperture facing upwards. The measurements were made using Infinity Analyze© software on images taken with an Infinity 1 camera on the same stereomicroscope. The measurements on the images were reproducible to ± <0.01 mm, but unavoidable slight tilting of the shells almost certainly caused minor additional loss of precision. Drawings were made using a Meiji drawing tube.

A representative list of the material studied is given in the Appendix, including specimens from England, C. and E. France and Malta used for comparisons; the full list is available from the authors. Abbreviations used for collections addi-

tional to those listed for the Appendix are as follows: ANSP= Academy of Natural Sciences of Philadelphia, U.S.A., SMF= Senckenberg Museum, Frankfurt, Germany.

RESULTS, WITH COMMENTS ON TAXONOMY AND HABITATS

Table I gives shell measurements of Iberian samples of *T. beckmanni* and *T. callicratis*, with comparative measurements of *T. cylindrica* from the French Pyrenees; Table II presents data on occurrence of apertural teeth in samples of >7 shells of *T. callicratis*; Fig. 1 gives drawings of representative shells of *T. beckmanni*, *T. callicratis* and *T. cylindrica*; Fig. 2 illustrates apertural teeth of *T. beckmanni* and *T. callicratis*; Fig. 3 is a graph of mean shell height versus mean shell breadth for selected populations. Distribution maps based on specimens examined are given as Figs. 4-6, for *T. beckmanni*, *T. callicratis* and *T. cylindrica* respectively. The synonymy presented below consists mainly of selected names that we discuss; PILSBRY (1920-1921) presented much more complete lists.

Genus *Truncatellina* R.T. Lowe, 1852

Type species: *Pupa linearis* R.T. Lowe, 1852, by monotypy.

Truncatellina beckmanni Quintana, 2010

Truncatellina beckmanni Quintana, 2010, Spira, 3, p. 153, figs. 4A-C. Type locality: Lloc de Monges (Ciutadella de Menorca, Illes Baleares). Holotype: Museu Diocesà de Menorca MDM-2703 (not seen).

Diagnostic characters: Aperture with three well developed teeth in all mature shells, the palatal tooth visible in frontal view of shell mouth, the parietal tooth large, well developed, forming tall lamellar ridge descending into aperture (Figs. 2A, C). Differs from toothed forms of *T. callicratis* in stronger teeth, relatively short and wide shell (height/breadth 1.4-1.9; shell breadth 0.79-1.00 mm, population means 0.85-0.94 mm); ribs on body whorl usually widely spaced.

Our specimens from Portugal and Andalucia (Figs. 1-4, Appendix) have been closely compared with topotypes of *T. beckmanni*. These populations have larger average shell dimensions than those from Menorca, but three of the smaller-shelled samples among them demonstrate much overlap (site P46 in Beira Litoral, sample 10747 from Estremadura, site P118 in Algarve) (Table I, Figs. 1, 3). The size and form of the apertural teeth and ribbing on the shells in Menorcan material can also be matched in samples from Portugal and Andalucia. The original description of *T. beckmanni* (QUINTANA, 2010: 155) states that "A diferencia de *T. purpuraia*, *T. beckmanni* no presenta callo parietal", but Fig. 4A in the same paper suggests there is at least a weakly developed parietal callus. Our material from Portugal and Andalucia often has a definite parietal callus, but sometimes none, its strength often appearing to correspond to the thickness and degree of calcification of the whole shell. Since Menorcan specimens are within the overall range of variation of all characters in samples from Portugal and Andalucia, we have no hesitation in regarding them all as conspecific.

T. beckmanni coexists with *T. callicratis* at several localities in Portugal (Beira Litoral, Estremadura) and Andalucia (Prov. Málaga), the detailed data being given in the Appendix. Where they coexist, all good adult specimens are readily assigned to one species or the other using characters set out in our diagnosis above and key below. Thus, *T. beckmanni* invariably has a longer parietal tooth, forming a tall lamella when fully developed (Fig. 2) and normally a shorter, wider shell with more widely spaced ribs (Figs. 1, 3, Table I).

T. beckmanni most closely resembles *T. klemmi* Zilch, 1962 (type-locality Cyrenaica,

Table I. Shell measurements for *Truncatellina beckmanni*, *T. callicratis* and *T. cylindrica*.
Tabla I. Medidas de la concha de Truncatellina beckmanni, T. callicratis *y* T. cylindrica.

Species	Sample no.	Region	Locality	N		Shell height	Shell breadth	height/ breadth	Teeth
Truncatellina:									
beckmanni		Menorca	data from Quintana (2010)	92	Min.	1.240	0.790		
				92	Max.	1.600	0.940		
				92	Mean	1.400	0.860	1.627	
				92	S.D.	0.080	0.034		
beckmanni	11296	Menorca	Lloc de Monges	1		1.298	0.842	1.542	
				1		1.384	0.844	1.640	
beckmanni	1984.90.2	Prov. Córdoba	2 km NE. of Cabra	1		1.511	0.896	1.686	
				1		1.519	0.921	1.649	
beckmanni	6989	Prov. Málaga	Sierra de San Jorge	4	Min.	1.593	0.913	1.708	
				4	Max.	1.658	0.966	1.770	
				4	Mean	1.630	0.940	1.735	
				4	S.D.	0.027	0.027	0.028	
beckmanni	1984.92.1	Prov. Málaga	1 km NW. of Puerto de Las Pedrizas	1		1.599	0.977	1.637	
beckmanni	P117	Algarve	E. of Santa Barbara de Nexe	8	Min.	1.467	0.890	1.645	
				8	Max.	1.618	0.937	1.780	
				8	Mean	1.544	0.907	1.703	
				8	S.D.	0.050	0.019	0.046	
beckmanni	P118	Algarve	3 km NNW. of Moncarapacho	20	Min.	1.336	0.832	1.606	
				20	Max.	1.630	0.913	1.777	
				20	Mean	1.474	0.870	1.694	
				20	S.D.	0.067	0.022	0.058	
beckmanni	1984.408.1	Algarve	5 km E. of Santa Caterina	1		1.406	0.851	1.652	
beckmanni	10747	Estremadura	Portinho da Arrábida	3	Min.	1.362	0.829	1.586	
				3	Max.	1.494	0.859	1.802	
				3	Mean	1.430	0.849	1.686	
				3	S.D.	0.066	0.017	0.109	
beckmanni	1984.419.12	Estremadura	7 km NE. of Portinho da Arrábida	1		1.373	0.878	1.564	
beckmanni	1984.418.1	Estremadura	5 km NE. of Portinho da Arrábida	1		1.430	0.885	1.616	
				1		1.483	0.894	1.659	
				1		1.526	0.924	1.652	
beckmanni	2007/16	Estremadura	Serra da Arrábida	1		1.459	0.885	1.649	
				1		1.659	0.946	1.754	
beckmanni	2010/P43	Estremadura	Fórnea	1		1.645	0.919	1.790	
beckmanni	P162	Estremadura	S. Bartolomeu	1		1.381	0.842	1.640	
beckmanni	2010.P64	Estremadura	1.5 km SE. of Livramento	64	Min.	1.263	0.843	1.467	
				64	Max.	1.645	0.999	1.819	
				64	Mean	1.509	0.911	1.655	
				64	S.D.	0.078	0.032	0.075	

Table I. Continuation.
Tabla I. Continuación.

Species	Sample no.	Region	Locality	N		Shell height	Shell breadth	height/ breadth	Teeth
beckmanni	2010.P41	Ribatejo	SE. of Moitas Venda	93	Min.	1.350	0.869	1.453	
				93	Max.	1.807	1.008	1.933	
				93	Mean	1.560	0.928	1.682	
				93	S.D.	0.080	0.028	0.084	
beckmanni	2008/P8	Beira Litoral	Capela Nostra Senora Covões	1		1.415	0.867	1.632	
beckmanni	2010/P46	Beira Litoral	1 km SW. of Ateanha	11	Min.	1.310	0.842	1.495	
				11	Max.	1.575	0.932	1.812	
				11	Mean	1.458	0.882	1.655	
				11	S.D.	0.086	0.028	0.108	
beckmanni	2010.P45	Beira Litoral	Vale da Couda	4	Min.	1.470	0.852	1.670	
				4	Max.	1.642	0.930	1.766	
				4	Mean	1.546	0.904	1..710	
				4	S.D.	0.073	0.036	0.044	
beckmanni	2010.P75	Beira Litoral	2 km WNW. of Ansião	12	Min.	1.424	0.880	1.525	
				12	Max.	1.661	0.975	1.825	
				12	Mean	1.522	0.916	1.663	
				12	S.D.	0.065	0.024	0.091	
beckmanni	2010.P73d	Beira Litoral	1.5 km WNW. of Ansião	10	Min.	1.539	0.904	1.640	
				10	Max.	1.712	0.960	1.840	
				10	Mean	1.605	0.930	1.727	
				10	S.D.	0.056	0.018	0.076	
callicratis	2011.P117	Algarve	2 km E. of Santa Barbara de Nexe	8	Min.	1.531	0.802	1.871	toothless
				8	Max.	1.918	0.894	2.145	
				8	Mean	1.649	0.839	1.966	
				8	S.D.	0.129	0.038	0.106	
callicratis	2011.P118	Algarve	3 km NNW. of Moncarapacho	59	Min.	1.261	0.764	1.572	toothless
				59	Max.	1.964	0.868	2.294	
				59	Mean	1.566	0.827	1.894	
				59	S.D.	0.129	0.022	0.133	
callicratis	2011.P104	Algarve	E. end of Rocha da Pena	22	Min.	1.337	0.765	1.737	mainly
				22	Max.	1.639	0.827	2.016	toothless
				22	Mean	1.502	0.797	1.884	
				22	S.D.	0.066	0.015	0.072	
callicratis	10750	Estremadura	Portinho da Arrábida	4	Min.	1.493	0.793	1.883	toothless
				4	Max.	1.709	0.835	2.047	
				4	Mean	1.564	0.805	1.941	
				4	S.D.	0.098	0.020	0.073	
callicratis	2010.P32	Estremadura	Serra de Montejunto	1		1.784	0.889	2.007	3-toothed
callicratis	P162	Estremadura	S. Bartolomeu	1		1.521	0.856	1.777	3-toothed
callicratis	2009.P14	Estremadura	above Grutas de Alvados	4	Min.	1.645	0.836	1.968	3-toothed
				4	Max.	1.900	0.880	2.159	

Table I. Continuation.
Tabla I. Continuación.

Species	Sample no.	Region	Locality	N		Shell height	Shell breadth	height/ breadth	Teeth
				4	Mean	1.758	0.865	2.032	
				4	S.D.	0.108	0.020	0.089	
callicratis	2010.P64	Estremadura	1.5 km SE. of Livramento	37	Min.	1.550	0.804	1.832	3-toothed
				37	Max.	2.037	0.960	2.273	
				37	Mean	1.773	0.874	2.027	
				37	S.D.	0.126	0.029	0.129	
callicratis	2010.P43	Estremadura	Fórnea	39	Min.	1.458	0.824	1.697	3-toothed
				39	Max.	2.031	0.957	2.163	
				39	Mean	1.715	0.873	1.965	
				39	S.D.	0.097	0.031	0.083	
callicratis	2011.P175	Ribatejo	just W. of Tomar	22	Min.	1.602	0.837	1.839	3-toothed
				22	Max.	1.964	0.927	2.187	
				22	Mean	1.787	0.881	2.028	
				22	S.D.	0.095	0.023	0.091	
callicratis	2010.P41	Ribatejo	SE. of Moitas Venda	13	Min.	1.654	0.838	1.933	3-toothed
				13	Max.	1.942	0.935	2.152	
				13	Mean	1.790	0.886	2.021	
				13	S.D.	0.088	0.030	0.069	
callicratis	2010.P79	Beira Litoral	1km SW. of Alfarelos	5	Min.	1.493	0.772	1.885	3-toothed
				5	Max.	1.727	0.861	2.006	
				5	Mean	1.606	0.826	1.943	
				5	S.D.	0.089	0.033	0.058	
callicratis	P45	Beira Litoral	Vale da Couda	1		1.711	0.848	2.018	3-toothed
				1		1.563	0.828	1.888	3-toothed
callicratis	2010.P78	Beira Litoral	1 km NW. of Verride	24	Min.	1.623	0.840	1.868	3-toothed
				24	Max.	2.089	0.914	2.387	
				24	Mean	1.859	0.880	2.112	
				24	S.D.	0.145	0.021	0.142	
callicratis	2010.P75	Beira Litoral	2 km WNW. of Ansião (ledge on crag)	54	Min.	1.457	0.812	1.748	3-toothed
				54	Max.	1.926	0.916	2.128	
				54	Mean	1.657	0.854	1.940	
				54	S.D.	0.103	0.023	0.103	
callicratis	2010.P73d	Beira Litoral	1.5 km WNW. of Ansião	9	Min.	1.696	0.850	1.899	3-toothed
				9	Max.	1.931	0.907	2.129	
				9	Mean	1.779	0.878	2.026	
				9	S.D.	0.066	0.019	0.068	
callicratis	2011.P170	Trás-os-Montes	NNE. of Rabal	1		2.007	0.912	2.201	toothless
				1		1.770	0.894	1.980	toothless
cylindrica	37070	Hautes-Pyrénées	8.2 km SW. from Gavernie	20	Min.	1.802	0.912	1.976	
				20	Max.	2.244	1.011	2.265	
				20	Mean	2.007	0.956	2.099	
				20	S.D.	0.104	0.023	0.080	

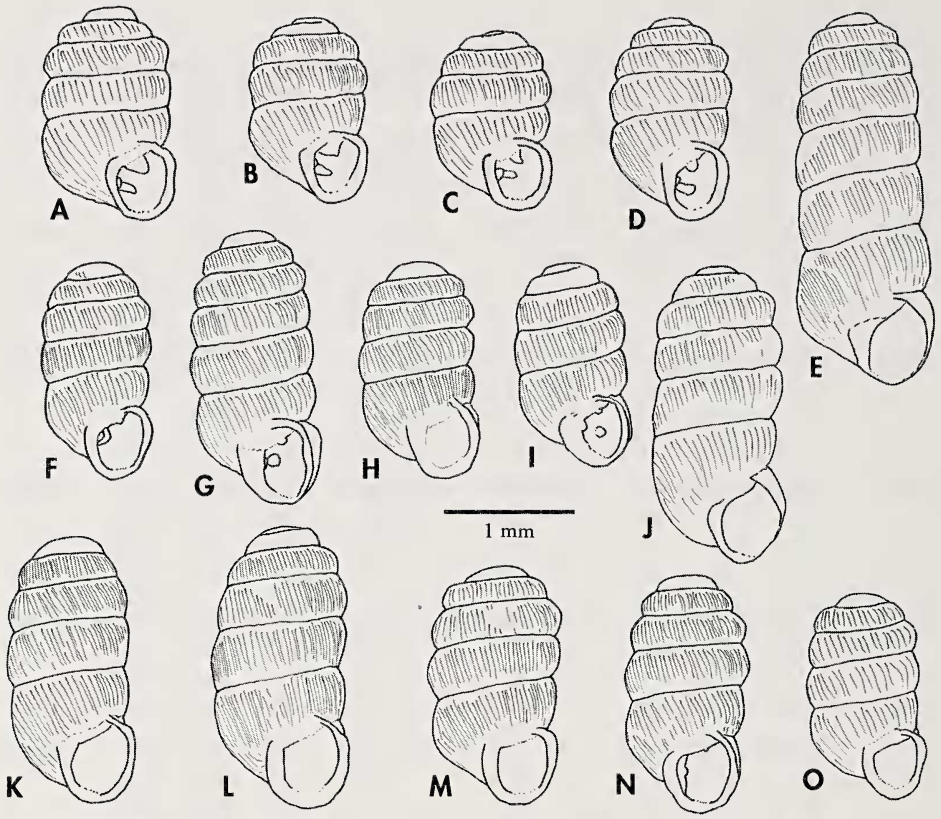

Figure 1. Drawings of representative shells of *Truncatellina* spp. A-D, *T. beckmanni*: A, Ribatejo, Portugal (site P41), B, Menorca (topotype, no. 11296), C, D, Beira Litoral, Portugal (site P46); E, *T.* cf. *callicratis*: Prov. Girona, Spain (no. 1983.147.20a); F-I, *T. callicratis*: F, G, Estremadura, Portugal (site P64, small and large shells from same population), H, Algarve, Portugal (site P118), I, Algeria (no. 1984.267.1); J, *T.* cf. *callicratis*: Prov. Girona, Spain (no. 1983.147.20a); K, L, *T. cylindrica*: K, Bedfordshire, England (no. 1977.140.1), L, Hautes-Pyrénées, France (collected 2001.06.28); M-O, *T. callicratis*: M, Morocco (no. 1986.311.04), N, Dorset, Great Britain (no. 1977.150.1), O, Morocco (no. 1986.80.4, from population with widely spaced ribs on shells). Note that shells G, I and N have been rotated slightly to show columellar tooth; other shells were drawn with aperture facing upwards. E, I and J had lost the periostracum, so the suture appears rather shallow; the other specimens had the periostracum ± intact. E and J are "overgrown" shells lacking thickened mature peristome, E with shallow suture, J with deep suture on part of shell. See Appendix for details of specimens figured.
Figura 1. Dibujos de conchas representativas de Truncatellina *spp. A-D,* T. beckmanni*: A, Ribatejo, Portugal (localidad P41), B, Menorca (topotipo, nº 11296), C, D, Beira Litoral, Portugal (localidad P46); E,* T. *cf.* callicratis: *Prov. Girona, España (nº 1983.147.20a); F-I,* T. callicratis: *F, G, Estremadura, Portugal (localidad P64, conchas pequeñas y grandes de la misma población), H, Algarve, Portugal (localidad P118), I, Argelia (nº 1984.267.1); J,* T. *cf.* callicratis: *Prov. Girona, España (nº 1983.147.20a); K, L,* T. cylindrica: *K, Bedfordshire, Inglaterra (nº 1977.140.1), L, Hautes-Pyrénées, Francia (recolectadas 28.06.2001); M-O,* T. callicratis: *M, Marruecos (nº 1986.311.04), N, Dorset, Gran Bretaña (nº 1977.1501.1), O, Marruecos (nº 1986.80.4, de una población con conchas con costillas muy separadas). Nótese que las conchas G, I y N se han girado ligeramente para mostrar el diente columelar; otras conchas han sido ilustradas mostrando la abertura hacia arriba. E, I y J han perdido el periostraco, por lo que la sutura parece bastante superficial; los otros ejemplares tenían el periostraco ± intacto. E y J son conchas de crecimiento anómalo faltándoles el peristoma típico de ejemplares maduros, E con sutura poco profunda, J con sutura profunda en parte de la concha. Ver apéndice para los detalles de los ejemplares figurados.*

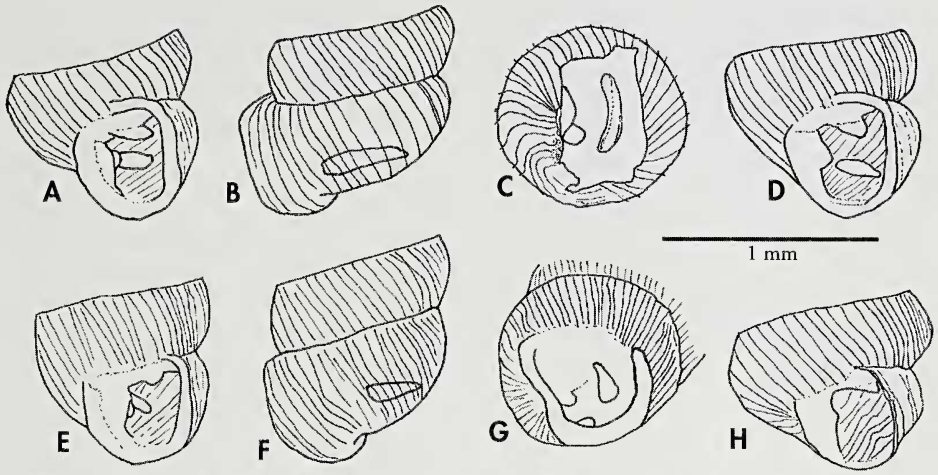

Figure 2. Drawings of apertural teeth of *Truncatellina* spp. A-D, H, *T. beckmanni* from Ribatejo, Portugal (site P41), E-G, *T. callicratis* from Estremadura, Portugal (site P64). A, D, E and H, show shell aperture facing approximately upwards, but rotated slightly to reveal columellar tooth; B and F, show back of body whorl with aperture facing downwards, the opaque white base of the palatal tooth being outlined; C, is view from below of an adult shell from which the peristome and palatal part of the aperture have been broken away to reveal the columellar tooth (left of centre) and full length of parietal tooth (right of centre), mouth of the aperture being at top of drawing; G, as C except that view is somewhat oblique, revealing full length of parietal tooth and top of palatal tooth; H, subadult shell with three small teeth, but peristome not thickened or reflected. See Appendix for details of specimens figured.

Figura 2. Dibujos de dientes aperturales de Truncatellina *spp. A-D, H,* T. beckmanni *de Ribatejo, Portugal (localidad P41), E-G,* T. callicratis *de Estremadura, Portugal (localidad P64). A, D, E y H, muestran la abertura de la concha orientada aproximadamente hacia arriba, pero ligeramente giradas para mostrar el diente columelar; B y F, muestran la parte posterior de la vuelta principal con la abertura orientada hacia abajo, la base blanca opaca del diente palatal se ha resaltado; C, concha adulta vista desde abajo en la que el peristoma y la parte columelar de la abertura se han roto para mostrar el diente columelar (a la derecha del centro), estando la boca de la abertura situada en la parte superior del dibujo; G, como C aunque esta vista es algo oblicua, revelando la longitud total del diente parietal y la parte superior del diente palatal; H, concha subadulta con tres dientes pequeños, aunque el peristoma no está engrosado ni reflejado. Ver apéndice para los detalles de los ejemplares figurados.*

Libya) and *T. purpuraria* Hutterer & Groh, 1991 (described from undated fossil or subfossil shells from Lanzarote, Alegranza and Fuerteventura in the eastern Canary Islands). *T. klemmi* differs from *T. beckmanni* in its wider shell (height 1.4-1.8 mm, breadth 1.0-1.2 mm) although our Portuguese sample with broadest shells (0.869-1.008, mean 0.928 mm: Table I) may nevertheless show slight overlap. The ribs on shells of *T. klemmi* are rather widely and regularly spaced as in *T. beckmanni*, but with broader, higher crests forming low lamellae.

Compared to our specimens of *T. beckmanni* from Portugal and Andalucia, *T. purpuraria* differs in having much more closely spaced ribbing on the shell and a rounded palatal tooth, whereas in *T. beckmanni* the palatal tooth is much longer than wide, forming a low lamellar rib extending back into the aperture (Fig. 2B). See above for comments on development of a parietal callus in *T. beckmanni*.

T. purpuraria was described as showing the closest relationship in conchological characters to Ethiopian species of the genus (*T. lardea* (Jickeli, 1875), *T.*

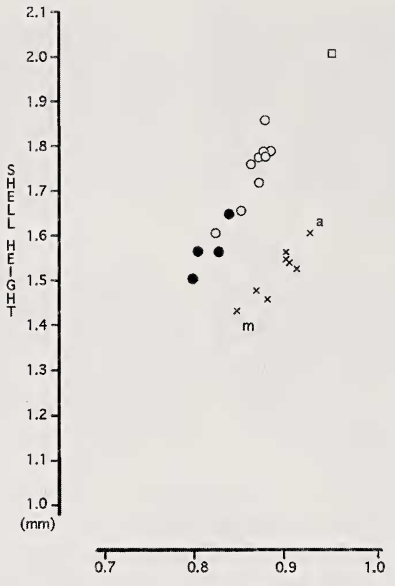

Figure 3. Graph of mean shell height and mean shell breadth for population samples of *Truncatellina* spp. x= *T. beckmanni* from Portugal, a= *T. beckmanni* from Andalucia, m= *T. beckmanni* from Menorca (data from QUINTANA, 2010), ○= *T. callicratis* from C. Portugal (populations with three apertural teeth), ●= *T. callicratis* from S. Portugal (populations mainly or entirely lacking apertural teeth), ❑= *T. cylindrica* from French Pyrenees.

Figura 3. Gráfico de la altura media y anchura media de la concha para las muestras de poblaciones de Truncatellina *spp.* x= T. beckmanni *de Portugal, a*= T. beckmanni *de Andalucía, m*= T. beckmanni *de Menorca (datos de QUINTANA, 2010),* ○= T. callicratis *de C. Portugal (poblaciones con tres dientes aperturales),* ●= T. callicratis *de S. Portugal (poblaciones casi o completamente desprovistas de dientes),* ❑= T. cylindrica *de los Pirineos franceses.*

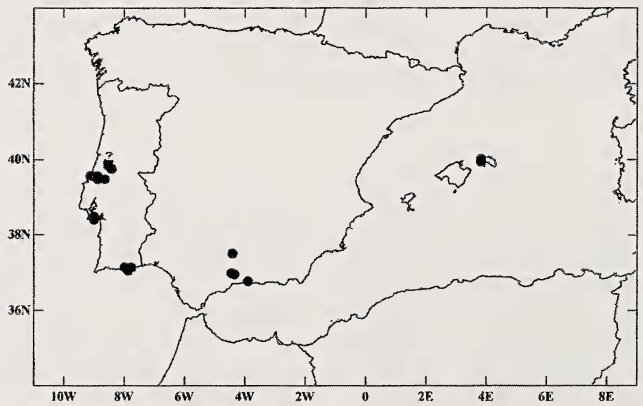

Figure 4. Map of distribution of *Truncatellina beckmanni*, based on specimens examined (except for some of the data from Menorca, from QUINTANA, 2010). ?= identification not certain because good adult shells not seen.

Figura 4. Mapa de distribución de Truncatellina beckmanni, *basado en los ejemplares examinados (excepto para algunos, recavados de los datos de Menorca, de QUINTANA, 2010). ?= identificación dudosa por no haber podido ver buenos ejemplares adultos.*

schilleri (Jickeli, 1875), *T. similis* (Jickeli, 1875)), and the same may apply to *T. klemmi* and *T. beckmanni*, if the similarities are not merely results of convergent evolution of shell characters. Of these species, *T. schilleri* and *T. similis* differ from *T. purpuraria* in having "palatal folds (not teeth!) ... only visible in an oblique view in the aperture, furthermore both are narrowly umbilicated". "*T. lardea* resembles *T. purpuraria* at first sight but is slightly larger ..., its palatal tooth is more elongated and – most striking – the costulation is much sparser" (HUTTERER AND GROH, 1991). *T. klemmi* was said to differ from *T. purpuraria* in being significantly wider (1.0-1.2 mm), sparsely but prominently costulated, with its crest-like teeth placed more deeply in the aperture (HUTTERER AND GROH, 1991: 8).

The habitats from which we have collected *T. beckmanni* are at 10-840 m elevation, mainly on limestone slopes with rock exposed more or less extensively as crags or screes. The sites mostly have open or incomplete vegetation cover, of herbs, grasses, or bushes. One atypical record was from crevices of walls alongside a river (Río Chillar, Nerja, Prov. Málaga). A second atypical record was of a single shell from a low, isolated, granite hill with crags and rather open low woodland (São Bartolomeu, 2 km SE. of Nazaré, Estremadura), a locality with some base in the soils because of calcareous sand blown in from surrounding low ground. *T. callicratis* was usually present with *T. beckmanni*, or close by, including at both of the atypical sites mentioned.

Truncatellina callicratis (Scacchi, 1833)

Turbo callicratis Scacchi, 1833, Osserv. Zool., p. 11. Type locality: Naples, Botanical Garden [Italy]. Types: unknown.

syn. *Pupa rivierana* Benson, 1854, Ann. Mag. Nat. Hist., (2), 13, p. 97. Type locality: Riviera regione Pedemontana, ad basin collium prope Nizza maritimam sub lapide [Italy].

Pupa strobeli Gredler, 1856, Verh. Zool.-bot. Vereins in Wien, 6, p. 114. Type locality: Klausen, southern Tyrol, on the garden hill of the Capuchin Fathers [Austria].

Vertigo muscorum var. *triplicata* Bourguignat, 1864, Malac. de l'Algérie, 2, p. 99, pl. 6, figs. 31-32. Type locality: Algérie, près de Bône, dans les alluvions de le Boudjimah, et dans celles de l'Harrach, près de Alger.

P.[*upa*] (*Isthmia*) *Scharffi* O. Boettger, 1879, Nachrbl. dtsch. Mal. Ges., 11 (No. 4-5, April-Mai), p. 51. Type locality: Genist ... am Ufer der Garonne [Bordeaux, France].

Pupa Strobeli var. *Scharffi* O. Boettger: anon., 1879 [October, or later], J. Conch., Lond., 2, p. 291. From "alluvium at Bordeaux".

Pupa strobeli var. *callicratis* Sc.: Westerlund, 1887, Fauna pal. Reg. Binnenconch., 3, p. 126.

Isthmia doumeti Letourneux and Bourguignat, 1887, Prodr. Malac. Tunisie, p. 110. Type locality: Tunis: drift debris of the Oued Sidi-Aich.

Isthmia rothi Reinhardt, 1916, Nachrbl. dtsch. Mal. Ges., 48, p. 164. Type locality: Greece, around Athens.

Truncatellina rivierana britannica Pilsbry, 1921, Man. Conch., 26, p. 77, pl. 8, figs. 13, 14. Type locality: Portland, Dorset, England. Holotype and paratypes at ANSP (not seen).

Truncatellina britannica Kennard and Woodward, 1923, Proc. Malac. Soc. Lond., 15 (6), p. 294.

Truncatellina brandti Zilch, 1962, Arch. Moll., 89 (1-3) [for 1960], 58, pl. 9, fig. 2. Type locality: Wadi Halgh el Asel zwischen Tokra und Tolmetta [Cyrenaica, Libya]. Holotype and paratypes at SMF.

Truncatellina lussinensis Štamol, 1995, Arch. Moll., 124 (1/2), p. 99, figs. 3, 4, 7, 8. Type locality: Croatia, the island of Lošinj, Veli Lošinj. Holotype no. 4993 and two paratypes no. 4994: Croatian Natural History Museum, Zagreb (not seen).

PILSBRY (1921) adopted the name *T. rivierana* for the species. However, he cited information from WESTERLUND (1887: 126) who obtained specimens from the original locality of *callicratis*, stated that it is a form of *strobeli* and accorded it varietal rank under that species (see above). Recent authors have

therefore used *callicratis* as the species name because it has priority.

Diagnostic characters: Apertural teeth 0-3 in mature shells, most populations being comprised mainly of shells with 0 or 3 teeth. When a palatal tooth is present it is visible with at least an oblique view into shell mouth; when a parietal tooth is present it is relatively small, not forming a tall lamellar ridge. Shell short to long (height 1.26-2.09 mm), usually relatively narrow (height/breadth 1.6-2.3; shell breadth 0.76-0.96 mm, population means 0.80-0.89 mm); ribs on body whorl usually closely spaced. The whorl profile tends to be higher and more rounded than in *T. cylindrica*.

Data on occurrence of apertural teeth in samples of this species are presented in Table II for the larger samples (>7 shells). Figure 5 shows the geographical pattern of occurrence of toothed, untoothed and partly toothed populations. However, Fig. 5 does not show populations which were not confidently identified as *T. callicratis*. The material excluded in this way from Fig. 5 mostly comprises small samples of shells lacking teeth, often old shells lacking the periostracum. These are likely to consist mainly of toothless *T. callicratis* with shells that do not clearly show deep sutures and a rounded whorl profile, probably because of the poor condition of the shells.

From Fig. 5 and Table II it is clear that untoothed populations predominate in the southernmost parts of the range, especially at low elevations in Morocco. Toothed and partly toothed populations are commoner in N. Algeria. Southern Iberia (Algarve and Andalucia) has untoothed populations or toothed populations with fewer than three teeth, whereas central and northern Iberia and France show mainly or entirely three-toothed (111) populations. Nevertheless, the northernmost population studied at Portland, Dorset, England has only a minority of 111 shells, accompanied by various types having one or two teeth, as pointed out long ago by Kennard and Woodward (1923) and confirmed by our data (Table II).

The literature as a whole has evidently treated *Truncatellina* lacking apertural teeth or with few weak teeth from S. Iberia and NW. Africa as belonging to *T. cylindrica* rather than *T. callicratis* (Bourguignat, 1864; Hidalgo, 1875, 1874; Pilsbry, 1920-1921; Nobre, 1941: 152-153; Martínez-Ortí and Robles, 2003; Ruiz *et al.*, 2006). This may be due partly to copying from the oldest literature which regarded *T. cylindrica* as the only species in its (sub) genus, an unsurprising assumption in the early years when most studies were carried out without adequate microscopes. That treatment was also maintained by some later workers adhering to an extraordinarily broad species concept, notably Nobre (1941).

Our own efforts to find *T. cylindrica* among numerous samples of untoothed *Truncatellina* from S. Iberia and NW. Africa have consistently been unsuccessful. Topotypical *T. cylindrica* from France differ from untoothed *T. callicratis* in characters set out in the diagnosis above and key below, principally larger size, shallower sutures and a flatter whorl profile (Table 1, Figs. 1, 3). Close comparisons of large samples of three-toothed *T. callicratis* from central Portugal (Beira Litoral, Ribatejo, Estremadura) with untoothed or predominantly untoothed populations in the Algarve shows that the latter actually average considerably smaller in size (Fig. 3, Table I) while sharing the deep sutures and rounded whorl profile characteristic of toothed *T. callicratis*. Furthermore, prolonged study of "apparently toothless" populations reveals that some include a proportion of weakly toothed shells, most often with just a columellar tooth present (e.g. P104 at Rocha da Pena in the Algarve; several Moroccan samples, notably 1986.326.1, 1984.153.4, 1984.139.1; a majority of the larger samples from N. Algeria) (Table II).

Recognition that populations of *T. callicratis* commonly show reduced or absent apertural teeth prompts reassessment of several nominal taxa listed as synonyms above.

The reduced teeth of British shells led Pilsbry (1921) to name them as *T. rivierana britannica*, and Kennard and

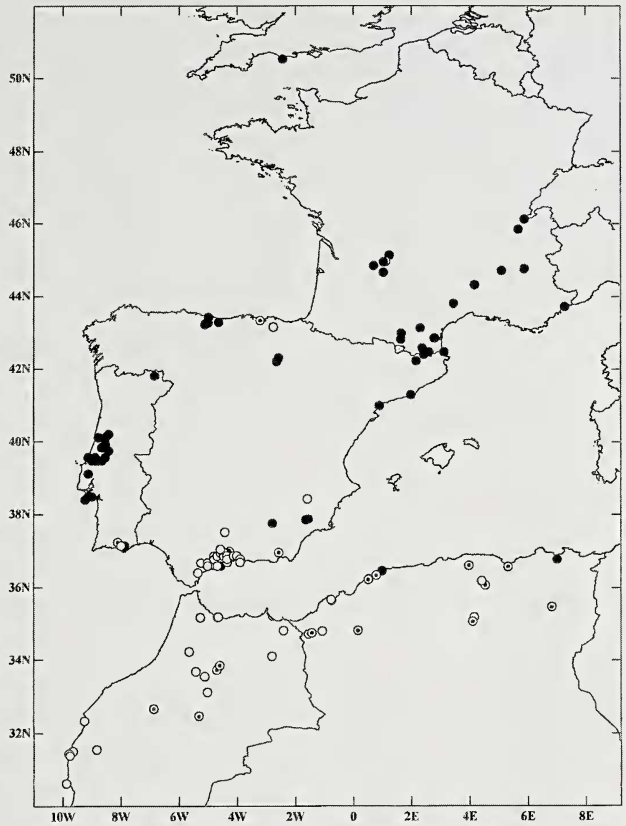

Figure 5. Map of distribution of *Truncatellina callicratis* based on specimens examined. ●= >80 per cent of shells with one or more apertural teeth; ○= no shells with apertural teeth; circles with central dot= 1-80 per cent of shells with apertural tooth or teeth, remainder lacking teeth.
Figura 5. Mapa de distribución de Truncatellina callicratis *basado en los ejemplares examinados.* ●= *>80 por ciento de las conchas con uno o más dientes aperturales;* ○= *conchas sin dientes aperturales; círculos con punto central= 1-80 por ciento de conchas con un diente o más, el resto sin dientes.*

WOODWARD (1923: 296) thought that other differences may exist to justify separation of *T. britannica* at species rank. Nevertheless, they admit to doubt over whether it is a variety, subspecies or distinct species, which they "have not yet had the opportunity of determining". Subsequent studies have failed to reveal other differences between British and continental material and the reduced apertural teeth now seem unimportant when the whole pattern of variability in occurrence of apertural teeth in *T. callicratis* is considered. Because a sample of British shells with reduced teeth can be matched by various samples from Iberia any nomenclatural recognition seems unwarranted.

PILSBRY (1921: 72) gave a muddled citation of "*Pupa strobeli* var. *scharffi* Boettger, Nachrbl. d. Mal. Ges., 1879, p. 51". In fact, at the reference given, O. BOETTGER (1879: 51) named *P.*[*upa*] (*Isthmia*) *Scharffi* based on three shells collected from river debris at Bordeaux by Robert Scharff. Later in the same year, Mr Scharff exhibited specimens at a meeting of the Conchological Society in Bradford, the account of which (ANON., 1879) gives the name as *Pupa Strobeli* var. *Scharffi*, "described by Dr. Boettger of Frankfort". T. von Proschwitz (in FALKNER *ET AL.*, 2002:

Table II. Data on occurrence of apertural teeth in samples of *Truncatellina callicratis*. Data are listed here for samples of >7 shells; *= shells from floodline debris. See text for methods used in scoring shells. A shorthand notation was used in scoring teeth of individual shells, taking the names in alphabetical order as columellar, palatal, parietal; thus *e.g.*, 111= all three teeth present, 000= no teeth present, 101= columellar and parietal present but not palatal.

Tabla II. Datos sobre la presencia de dientes aperturales en muestras de Truncatellina callicratis. *Se listan los datos de las muestras de >7 conchas; *= conchas de sedimentos de ríos. Ver el texto para los métodos usados para contabilizar las conchas. Una anotación taquigráfica se usó para contar los dientes de las distintas conchas, ordenando los nombres alfabéticamente como columelar, palatal, parietal; así p. ej., 111= los tres dientes presentes, 000= ningún diente presente, 101= columelar y parietal presentes, aunque no el palatal.*

Country, Province	Site no., Specimen no. or date	Teeth: 000	100	010	001	110	011	101	111	Total
Great Britain, Dorset	1976.194.1, 1977.150.1, 1982.138.1	–	4	–	–	1	–	2	2	9
Great Britain, Dorset	from Kennard and Woodward (1923)	2	77	–	–	26	–	–	5	110
France, Ain	1976.228.7a, 1976.228.23	2	–	1	–	4	1	–	11	19
France, Ain	1987.2.1, 1987.2.2	2	–	–	–	–	–	–	30	32
France, Dordogne	1981.13b.7	–	–	–	–	3	1	–	9	13
France, Dordogne	1981.14b.2, 1981.14b.5	4	–	–	–	1	1	2	7	15
France, Drôme	1985.368.1	–	–	–	–	–	2	1	13	16
France, Ariège	1981.55.1	–	–	–	–	5	–	–	4	9
France, Pyrénées-Orientales	1981.58.2	–	–	–	–	–	–	–	16	16
France, Pyrénées-Orientales	1981.67.4	–	–	–	–	10	–	–	43	53
France, Pyrénées-Orientales	1981.73.1	–	–	1	–	3	–	–	8	12
N. Spain, Asturias	E159	1	–	–	1	–	3	–	36	41
N. Spain, Cantabria	2001.05.22	–	–	–	–	–	1	–	11	12
N. Spain, Girona	2001.06.16	–	–	1	–	13	4	–	89	107
*N. Spain, Girona	1983.147.20, 1983.147.21	36	–	–	–	–	–	–	20	56
N. Spain, Tarragona	1984.65.1	2	4	–	–	4	–	5	16	31
C. Portugal, Beira Litoral	P75	–	–	–	–	–	–	–	46	46
C. Portugal, Beira Litoral	P78	–	–	–	–	–	–	–	20	20
C. Portugal, Beira Litoral	NE4849	–	–	–	–	–	–	–	23	23
C. Portugal, Beira Litoral	NE5051	–	–	–	–	–	–	–	19	19
C. Portugal, Beira Litoral	NE3218	1	–	–	–	–	–	–	8	9
C. Portugal, Ribatejo	P41	–	–	–	–	–	–	–	9	9
C. Portugal, Ribatejo	P175	–	–	–	–	–	–	–	15	15
C. Portugal, Estremadura	P64	2	–	–	–	–	–	–	28	30
C. Portugal, Estremadura	P43	–	–	–	–	–	–	–	36	36
S. Portugal, Algarve	P104	14	8	–	–	–	–	–	–	22
S. Portugal, Algarve	P118	59	–	–	–	–	–	–	–	59
S. Portugal, Algarve	P117	8	–	–	–	–	–	–	–	8
Malta, Gozo	2005.03.17	–	–	1	–	2	1	–	30	34
Malta, Malta	2005.03.18	1	–	–	–	–	1	–	13	15
Algeria	1984.175.2	6	–	–	–	–	–	2	–	8
Algeria	1984.176.2	11	3	–	–	–	–	2	–	16
Algeria	1984.256.2	19	4	–	–	–	–	–	–	23

Table II. Continuation.
Tabla II. Continuación.

Country, Province	Site no., Specimen no. or date	Teeth: 000	100	010	001	110	011	101	111	Total
Algeria	1984.267.1	1	–	–	–	–	–	–	10	11
Algeria	1984.293.2	11	3	–	–	–	–	3	–	17
Algeria	1984.307.1	21	3	–	1	–	–	–	–	25
Algeria	1984.316.1	15	2	–	–	–	–	2	–	19
Algeria	1984.338.4	79	14	–	–	–	–	–	1	94
Algeria	1984.357.2	24	11	–	–	–	–	1	–	36
Algeria	1984.358.1	12	9	–	–	–	–	–	–	21
Algeria	1984.367.3	38	3	–	–	–	–	–	–	41
Morocco	1984.139.1	55	12	–	–	–	–	1	–	68
Morocco	1984.153.4	40	6	–	–	–	–	1	–	47
Morocco	1986.156.6	24	1	–	–	–	–	–	–	25
Morocco	1986.162.08	14	–	–	–	–	–	–	–	14
Morocco	1986.164.01	26	–	–	–	–	–	–	–	26
Morocco	1986.326.1	23	2	–	–	–	–	–	–	25

11) described additional records of this taxon in SW. France along with intermediates linking it to typical *T. callicratis*.

There is nothing in the description of *Isthmia doumeti* Letourneux and Bourguignat, 1887 from Tunisia to show that it is anything other than the toothless form of *T. callicratis* that predominates further west in north Africa over large areas of Morocco and Algeria, so it is regarded as a synonym of the latter name. HUTTERER AND GROH (1991: 19) listed shells from Oued Chair in Algeria (SMF) that were named as *T. doumeti* and, as noted above, that taxon was also reported from near Barcelona ("Altimira, 1969", cited by BECH, 1990); both of these are also likely to be referable to toothless forms of *T. callicratis*.

Isthmia rothi Reinhardt, 1916 from Greece was said to differ from *T. cylindrica* "by the compact structure, the peculiar form, wider above, the sharp, widely spaced striation, more convex whorls and deeper suture" (PILSBRY, 1921: 70). This taxon also seems likely to be based on a toothless form of *T. callicratis*. IRIKOV (2008) reported *T. rothi* new for Bulgaria, describing and figuring toothless shells (height 1.2-1.9 mm, diameter 0.8-0.9 mm) that are a good match for toothless *T. callicratis*, with rounded whorls and a deep suture.

Truncatellina brandti was described from more than 38 shells from several localities in Cyrenaica. Its shells lack teeth and measure 1.4-1.7 mm high and 0.8 mm wide. Although showing rather strong and widely spaced ribbing, this can be matched in our Algerian material assigned to untoothed forms of *T. callicratis* and they are closely similar in the deep sutures and rounded whorl profiles.

Truncatellina lussinensis Štamol, 1995 was described from a total of 12 shells found within an area about 500 m across. The twelve specimens are large (1.95-2.75 mm high, 0.79-1.00 mm in breadth), but "unfortunately there was only one satisfactory adult specimen among all twelve specimens" (ŠTAMOL, 1995: 100). The published drawings and photographs show that the whorl profiles and ribbing of the long shells are generally similar to those of *T. callicratis*. The author refers to the phenomenon of abnormalities in the shells of Pupoidea including *Truncatellina cylindrica* as described by GEYER (1912), including larger overall size, a larger number of whorls

and an incomplete (i.e. unreflected, unthickened) edge to the aperture. He commented as follows on the "possibility of regarding *T. lussinensis* as a form of gigantism in *T. callicratis*. [and that] The suggestion could be supported by the fact that *T. lussinensis* is invariably found in small numbers together with numerous typical specimens of *T. callicratis*. However, the specimen with a complete apertural edge refutes this suspicion, as does the appearance of *T. lussinensis* on a relatively large number of sites within the Veli Lošinj area". All the specimens described by Štamol were from the collection of France Velkovrh housed in the museum at Zagreb and no information is available on whether the collector made special efforts to seek out the large shells.

The present study found that "overgrown" abnormalities may recur repeatedly within populations of *T. callicratis* (e.g. 5 shells accompanying a total of 36 normal untoothed adults in 1983.147.20a from floodline debris in Prov. Girona; Figs. 1E, J). They resemble normal shells in depth of the suture, the whorl profile and ribbing, but have extra whorls and an unthickened peristome lip, as if shell growth has continued for longer than normal. Despite the occurrence of a "complete apertural edge" in one of the twelve specimens of *T. lussinensis*, it seems safe to regard the taxon as based on "overgrown" *T. callicratis* from its population known to be present in the same area.

In S. France and Iberia we have found *T. callicratis* at 10-1130 m elevation, mainly at sites with exposed limestone [including "marble", "dolomite" or "travertine"], such as on or about crags, on rocky slopes or on screes, but our search efforts tended to be focused on these habitats. Fewer records were from ruins and old limestone walls (2), a grassy roadside bank with no rocks (1), beside small irrigation channels in an area of slaty rock (1), sandstone rocks (2), calcareous sandstone (1), other siliceous rock (1) and a low granitic hill in an area receiving wind-blown calcareous sand (1). Its sites usually had incomplete or rather open cover of vegetation, typically of herbs, grasses or patchy bushes, but a few records were in places shaded by scrub or inside woodland.

Collections from Morocco and Algeria were made from 20-2200 m elevation, ranging from sites on sea-cliffs up to altitudes of 1760 and 2200 in the Moyen Atlas. Rocky limestone habitats predominated (21 sites), with other rocky sites recorded over varied sedimentary lithologies (calcareous sandstone (6), sandstone (3), shale (2), conglomerate (1)). The minority of sites with few or no rocks included a roadside bank (1) and a wooded hillside (1) both in a sandstone region, sandy sea-cliffs (1), calcareous clay slopes (1), sand dunes with some limestone boulders (1) and flat soil in a limestone region (1). Most of the localities had open vegetation, with a few inside open woodland or scrub.

Truncatellina cylindrica (A. Férussac, 1821)

Vertigo cylindrica A. Férussac, 1821, Tabl. Syst., p. 64. Type locality: France. Based on *Pupa muscorum, a* of Draparnaud, 1806, Hist. Nat. Moll. terr. et fluv. de France, p. 59, pl. 3, figs, 26, 27 in part (non Linnaeus), but with qualification added by Férussac of "bouche sans dents".

syn. *Truncatellina arcyensis* Klemm, 1943, Arch. Moll., 75 (2/3), p. 100. Type locality: Département Yonne, N. Avallon, S. end of road tunnel near Arcy sur Cure [France]. Holotype in Naturhistorisches Museum, Wien (Austria), collection Klemm 8378 (not seen).

Diagnostic characters: Apertural teeth always lacking. Compared to forms of *T. callicratis* lacking apertural teeth, shells relatively large (height 1.80-2.24 mm), shells usually wider (breadth 0.91-1.01 mm), sutures relatively shallow, whorl profile lower and somewhat flatter.

The discussion of *T. callicratis* above points out that it has often been reported erroneously as *T. cylindrica* in the

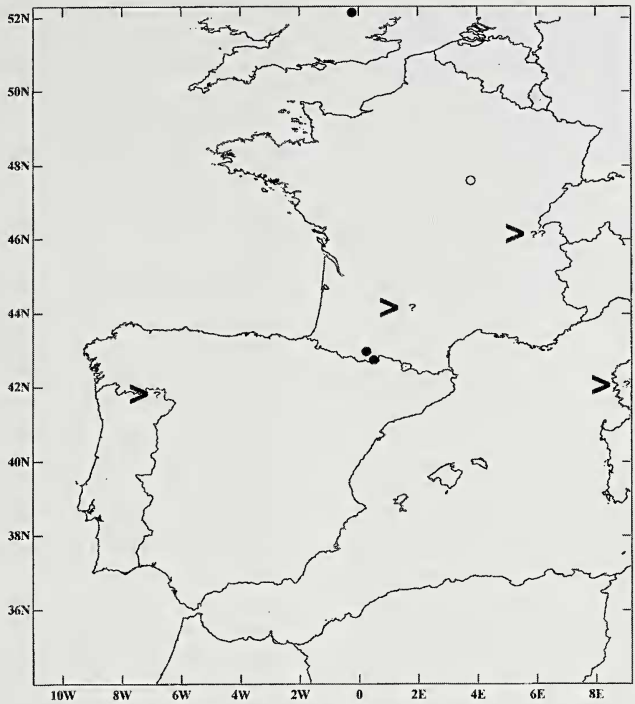

Figure 6. Distribution map of *Truncatellina cylindrica* based on specimens examined. ●= typical *T. cylindrica*; ○= shells showing characters of *T. arcyensis* (see text); ?= identification not certain.
Figura 6. Mapa de distribución de Truncatellina cylindrica *basado en los ejemplares examinados.* ●= T. cylindrica *típicos;* ○= *conchas que muestran caracteres de* T. arcyensis *(ver texto); ?= identificación dudosa.*

past from Iberia and NW. Africa. In the present study, the southernmost records of material confidently identified as *T. cylindrica* were from the French side of the Pyrenees, with only tentative records based on very few shells from further south at single localities in Corsica and NE. Portugal (Fig. 6, Appendix).

RUIZ *ET AL.* (2006: 242-243) mapped *T. cylindrica* as having a range in Andalucia more widespread than that of *T. callicratis*. However, the short description of *T. cylindrica* stated "sin dientes aperturales, aunque puede aparecer algún pliegue rudimentario" which suggests misidentification of weakly toothed *T. callicratis*, since *T. cylindrica* at its north- and central European localities always lacks teeth. Furthermore, their photos show a shell that may have carried on growing without forming a peristome lip (cf. the discussion of *T. lussinensis* above); it has deeper sutures and more swollen whorls than in *T. cylindrica*.

T. arcyensis Klemm, 1943 is known mainly from three localities in Dept. Yonne, France, with a single shell reported from river deposits in Switzerland (HAUSSER, 2005). Although treated as a valid species by recent authors (KERNEY AND CAMERON, 1979; FALKNER *ET AL.*, 2002; GARGOMINY AND RIPKEN, 2011) it resembles *T. cylindrica* rather closely in all characters other than a supposedly higher shell (2.2-2.4 mm, cf. 1.8-2.0 mm in *T. cylindrica*: KLEMM, 1943; KERNEY AND CAMERON, 1979; HAUSSER, 2005) and lack of ribs on the shell. However, a

topotype of *T. arcyensis* figured by Gargominy and Ripken (2011: Pl. 13D) clearly shows weak ribbing with similar spacing and orientation to that in *T. cylindrica*, and the mature shell involved is apparently only *ca* 1.76 mm high (little larger than the *T. cylindrica* figured in Pl. 13C of the same publication, which was collected at Mailly-le-Château in Dept. Yonne). A sample of 26 shells from Nailly Saint-Moré in Dept. Yonne collected in 1983 (NMW.Z. 1993.052.09392) is intermediate between *T. cylindrica* and the supposed characters of *T. arcyensis*. Their shell heights of 1.708-2.062 mm are well within the range of *T. cylindrica* (cf. heights up to 2.244 mm from a population with mean height of 2.007 mm (n= 20) measured during the present study: Table I) and shell breadth is also similar to that of *T. cylindrica*. Ribbing was present on all of the 26 shells, but markedly weaker (lower) than usual in *T. cylindrica;* this ribbing was almost lacking on parts of the body whorl of some fresh shells but present over all of the body whorl on others. *T. arcyensis* is therefore regarded as a weakly ribbed local form of *T. cylindrica* and placed as a synonym of that species here, although subspecific status might be justifiable. The clear differences between these taxa in shell height and ornamentation described in the literature apparently do not exist: even some topotypical *arcyensis* differ from *T. cylindrica* only in having weaker ribbing, and localities elsewhere in Dept. Yonne have more obviously intermediate shells, or typical *T. cylindrica*.

As noted above, the nearest records to the Iberian Peninsula accepted for *T. cylindrica* in this study are from the French Pyrenees. These were at elevations of 900 m and 1975 m, on rocky limestone slopes with open vegetation of grasses and herbs. It seems quite likely that the species will eventually be confirmed as occurring at least in northern Spain, most likely perhaps in montane habitats, but our study emphasises that great care will be needed to distinguish *T. cylindrica* from untoothed forms of *T. callicratis*. Further north in Europe, *T. cylindrica* occurs widely in very dry calcareous grassy places, characteristically among *Sedum* or *Artemisia*, often on screes, among rocks, or occasionally on sand dunes (Kerney and Cameron, 1979). Numerous specimens we have studied from Potton, Bedfordshire, England were from a dry sandy south-facing bank with cover of short herbaceous vegetation, but it no longer occurs there. In Poland it is commoner and occurs also in habitats of anthropogenic origin, in pastures, on railway embankments and on balks [banks] (Pokryszko, 1990: 224). In Asia and eastern Europe it occurs in steppe and semi-desert areas (Shileyko, 1984).

DISCUSSION

The apertural teeth of the *Truncatellina* species occurring in SW Europe and NW Africa are developed only as the growing shell approaches or reaches full size; small juvenile shells invariably lack teeth. In *T. beckmanni* all three teeth begin to grow before the peristome lip is thickened or reflected (Fig. 2H), whereas the smaller teeth of *T. callicratis* form as the peristome matures or later. Pokryszko (1990: 146) suggested that in *Truncatellina* the palatal tooth forms later than the columellar and parietal teeth, despite it being more deeply situated. She illustrated this in *T. costulata* (Nilsson, 1822) (cf. her Fig. 5 on p. 141), but does not make it clear that sufficient material of any other toothed *Truncatellina* species was examined during her study of Polish Vertiginidae to confirm that it is more generally applicable. Kennard and Woodward (1923: 295) had previously come to a different conclusion with British *T. callicratis "britannica"*, arguing for a columellar, palatal, parietal, sequence of development. They comment that: "The columellar tubercle, which is the most conspicuous as a rule, appears to form first, when the shell has come to full growth. The palatal tubercle

Table III. Summary of data on occurrence of shells with only one or two apertural teeth in samples of *Truncatellina callicratis*, based on totals given in Table II. For row (a), χ^2= 104.85, 5 d.f., *P*= <0.001; for row (b), χ^2= 337.64, 5 d.f., *P*= <0.001; for row (c), χ^2= 287.91, 5 d.f., *P*= <0.001.
Tabla III. Resumen de los datos sobre la presencia de conchas con sólo uno o dos dientes aperturales en muestras de Truncatellina callicratis, *basado en los totales que se dan en la Tabla II. Para la fila (a),* χ^2= *104,85, 5 d.f., P= <0,001; para la fila (b),* χ^2= *337,64, 5 d.f., P= <0,001; para la fila (c),* χ^2= *287,91, 5 d.f., P= <0,001.*

Row	Population with teeth:	Numbers of shells with:						Total
		100	010	001	110	011	101	
(a)	Mainly 111	4	4	1	45	15	8	(77)
(b)	Mainly 000	81	0	1	0	0	12	(93)
(c)	British (mainly 1 or 2 teeth)	81	0	0	27	0	2	(110)

develops next, and later the parietal (though we have seen a specimen with parietal but no palatal tubercle) completing the typical three in the old age of the snail".

Our data on occurrence of teeth in numerous populations of *T. callicratis* (Table II) apparently shed more light on sequences of tooth development. Only shells lacking one or two of the three teeth are likely to be informative and the data on these is summarised in Table III, along with results of some statistical tests. The following comments on relative frequencies of the different combinations with one or two teeth (i.e. "partly toothed combinations") assume there is no resorption of teeth after they grow, a possibility that is reconsidered below.

In the predominantly three-toothed populations [111], 110 is commonest (n= 45) of the partly toothed combinations and 001 rarest of all (n= 1), suggesting the parietal tooth is commonly the last to grow and very rarely the first to grow. Both 100 (4) and 010 (4) are equally uncommon, whereas 110 is much commoner (45), implying that simultaneous growth of columellar and palatal teeth is much commoner than either of these growing before the other. Thus the usual sequence would appear to be columellar and palatal growing simultaneously, then the parietal growing last. This is different to Pozkryszko's proposed sequence described above (i.e. columellar and parietal growing together, with palatal last) and more like Kennard and Woodward's sequence (columellar first, palatal second, parietal last) but also differing from the latter in that columellar and palatal usually grow together rather than in succession. Nevertheless, a significant proportion of shells deviate from the commonest pattern of development, as revealed by a significant number with 011 (n= 15), which either would not develop a columellar tooth, or would do so later than normal.

Shells in predominantly untoothed populations [000], have 100 as much the commonest of the partly-toothed combinations (n= 81, out of total n= 82 for all single-tooth possibilities). Thus they much more often grow a columellar tooth than any other tooth. If a second tooth is grown it is normally the parietal (n= 12 for 101) not palatal (n= 0 for 110). Developing all three teeth (111) in these populations is very rare (n= 1). Only a single shell in this group of populations is out of step with the main pattern (n= 1 for 001, i.e. the parietal is the only tooth present).

Pooling all available data for British populations (from Dorset) reveals that these, uniquely, appear to grow a columellar tooth first (n= 81 for 100); sometimes either adding a palatal as the second tooth or growing it simultaneously with the columellar (n= 27 for 110). Only rarely are all three teeth

grown (n= 7 for 111). A few shells appear to be out of step with the main trend (i.e. n= 2 for 101). These data tend to support KENNARD AND WOODWARD'S (1923) conclusion on the sequence of tooth growth (columellar grows first, palatal second, parietal last), but emphasise that finally developing all three teeth is atypical, not the usual reward for achieving "old age".

Hence characteristic overall patterns of tooth development appear to exist, albeit different in predominantly three-toothed and predominantly untoothed populations and different again in Britain. There may therefore be no need to consider resorption of teeth as a possible process affecting the number and location of teeth seen in shell specimens, although some "out of step" data could have this explanation.

It might be argued that the different sequence of tooth development in predominantly three-toothed and predominantly untoothed groups of populations may point to a more significant genetic difference between them than should occur in conspecifics. However, the considerable proportion of shells that do not conform to the commonest pattern of development (minima of 15 in three-toothed group, of 1 in untoothed group) would cast doubt on any such simple division into two groups, as would the peculiarities in development revealed among the closely studied British population.

The functional role played by apertural teeth in Pupillacea and other land snails has not been satisfactorily explained, although several plausible suggestions have been made (PILSBRY, 1948; SOLEM, 1972, 1976; SHILEYKO, 1984; POKRYSZKO, 1990), which need not be mutually exclusive. Narrowing the aperture to make attacks by predatory invertebrates more difficult was discussed by SOLEM (1972, 1976) and a more general function in strengthening the aperture is possible in various species. Differing functions for the teeth in different positions were suggested by SHILEYKO (1984): the columellar aiding action of the columellar retractor muscle so as to facilitate movements and carrying the shell; the parietal dividing the pulmonary cavity into two parts that have different functions; the palatal protecting the pallial complex against pressure from neighbouring organs; all teeth may also assist in squeezing mucus from the mantle as the snail withdraws into the shell, this mucus contributing to the epiphragm. Nevertheless, POKRYSZKO (1990: 146) pointed out that teeth tend to be reduced in some Vertiginidae and the "possible role of the knob-shaped and deeply situated palatal tooth in *Truncatellina* is completely obscure."

In attempting to understand the functional significance of apertural teeth in *Truncatellina*, it may be relevant that they only develop in fully-grown snails. The large teeth of species such as *T. beckmanni* may subserve various functions among those suggested for other Pupillacea above, such as predator avoidance, partitioning the aperture, protecting organs and helping to carry, move and orientate the shell. It is noteworthy that the large teeth of this species are consistently present and vary little in size and shape (although position of the palatal tooth may vary, cf. Figs. 2A, D). In contrast, the smaller teeth of *T. callicratis* can be developed or not and whole populations have none, as do all individuals in *T. cylindrica* and other "untoothed" species of the genus. It is therefore possible that the variability in number, position, size and developmental sequence of teeth in *T. callicratis* are a reflection of weak or non-existent selection pressures. In their small and possibly vestigial condition the teeth might be functionally unimportant, or almost so, perhaps developing only through pleiotropic action of genes controlling other more important effects.

It is convenient in constructing bipartite keys to *Truncatellina* species to make an initial separation of species with and without teeth (as in PILSBRY, 1920-1921; HUTTERER AND GROH, 1991: 13; HAUSSER, 2005) and we maintain this tradition in our own "artificial" key below. Nevertheless, development of apertural teeth in *T. callicratis* is variable both within and between populations as

described above, prompting a wider reassessment of the significance of teeth in *Truncatellina*. The great intraspecific variability in one of the species implies that presence or absence of teeth should not be regarded as decisively important in showing phylogenetic affinities within the genus. Indeed, a reliable phylogeny based on a combination of molecular-genetic and morphological studies now needs to be established and this should allow reassessment of the taxonomic value of teeth and other morphological characters among the species.

Key to identification of *Truncatellina* species in W Europe and NW Africa

This key covers all species occurring in England, W. and C. France, Spain, Portugal, Morocco and Algeria, but not all taxa from the Alps or Macaronesia. The characters used are those of adult shells with a fully formed peristome lip (reflected and somewhat thickened). Identification will be more reliable if it is based on a sample of shells from each local population.

1 - Shell with 1-3 apertural teeth 2
- Shell without apertural teeth 4

2 - Palatal tooth well developed but deeply inserted, so not visible with frontal view of shell mouth (usually visible externally as opaque whitish mark); shell narrow, breadth averaging *ca* 0.75 mm; SW. France, E. Spain . . . . . *T. claustralis*
- Palatal tooth well developed, weak or absent, visible with at least an oblique frontal view of shell mouth when present; shell usually wider, breadth 0.76-1.00 mm (population means 0.80 mm or more) 3

3 - Parietal tooth large, well developed, forming tall lamellar ridge descending into aperture (Figs. 2A, C); shell short and relatively wide (height/breadth 1.4-1.9); shell breadth 0.79-1.00 mm (population means 0.85-0.94 mm); ribs on body whorl usually widely spaced . . . . . *T. beckmanni*
- Parietal tooth medium-sized, small or absent, not forming tall lamellar ridge descending into aperture (Figs. 2E, G); shell short to long, usually relatively narrow (height/breadth 1.6-2.3); shell breadth 0.76-0.96 mm (population means 0.80-0.89 mm); ribs on body whorl usually closely spaced . . . . . *T. callicratis*

4 - Sutures relatively shallow*, whorl profile lower and somewhat flatter*; shells relatively large, height 1.80-2.24 mm; shells usually wider, breadth 0.91-1.01 mm; apertural teeth always lacking . . . . . *T. cylindrica*
- Sutures relatively deep*, whorl profile higher and more rounded*; shells small to large, height 1.26-2.09 mm; shells usually narrower, breadth 0.76-0.96 mm; small apertural teeth sometimes present in similar shells from same population . . . . . *T. callicratis*

*Note that only shells with the periostracum intact should be compared. Comparison of fresh shells with old shells that have lost the periostracum will be misleading.

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APPENDIX. LIST OF REPRESENTATIVE MATERIAL STUDIED

Most specimens are listed for the rarer species, but mainly one for each province for the commoner *T. callicratis*, except in Algeria and Morocco where there are few published records. A full list with data on habitats and altitudes is available from the authors. Data are listed in sequence for each species as country, province, locality name, latitude and longitude or U.T.M. grid reference, date, collectors' initials, collector's field number, collection where housed, registration number if any, number of shells or specimens (immature or adult), additional comments (if any). To save space, identical information on species, country and province is not repeated; a semi-colon is used only to separate each sample. Abbreviations: ÁDO= Álvaro De Oliveira, CÁDO= Collection of Álvaro De Oliveira, CGAH= Collection of G.A. and D.T. Holyoak, CJSTA= Collection of J.S. Torres Alba, DTH= D.T. Holyoak, GAH= G.A. Holyoak, JQ= J. Quintana, JSTA= J.S. Torres Alba, MH= M. Holyoak, MBS= M.B. Seddon, MPK= M.P. Kerney, NMW.Z.= Department of BioSYB, National Museum and Gallery of Wales, Cardiff, U.K., RBGW= R.B.G. Williams; sh= number of shells (ad= good adult shells, i.e. peristome with lip developed, aperture not obscured by debris, apex and peristome unbroken; br= broken shells; imm= immature shells; old= old shells; plugged= inside of aperture obscured by debris so locations of one or more teeth not seen); sp= number of specimens in alcohol; ?= species identity uncertain.

T. beckmanni: Portugal, Algarve, 5 km E. of Sta. Caterina, 29S PB11, 1984.08.22, DTH, MH & MBS 1984.408.1, NMW.Z.1993.052.10221, 3 sh (2 ad 1 br, 1 imm br); *ca* 2 km E. of Santa Barbara de Nexe, 29S 059428/410732, 2011.02.03, GAH & DTH P117, CGAH, 8 sh; *ca* 3 km NNW. of Moncarapacho (just S of A22), 29S 060695/410771, 2011.02.04, GAH & DTH P118, CGAH, 20 sh; Beira Litoral, Capela Nostra Senora Covões, 29S 05511/44073, 2008.09.01, GAH P8, CGAH, 1 sh; Vale da Couda (SE. of Almoster), 29S 05487/44103, 2010.05.29, GAH & DTH P45, CGAH, 4 sh; *ca* 1 km SW. of Ateanha village (E. of Alvorge), 29S 05498/44262, 2010.05.29, GAH & DTH P46, CGAH, 11 sh; *ca* 0.5 km S. of IC8 at *ca* 2 km WNW. of Ansião, 29S 054642/441843, 2010.09.26, GAH & DTH P73, CGAH, 12 sh; Estremadura, *ca* 5 km NE. of Portinho da Arrábida, 29S NC06, 1984.08.24, DTH, MH & MBS 1984.418.1, NMW.Z.1993.052.10329, 6 sh (3 ad); Serra da Arrábida, 29S 05000/42574, 2007.05.18, GAH 2007/16, CGAH, 1 sh; cliffs over Portinho da Arrábida, Setúbal, 29S NC05, 2009.09., JSTA 10747, CGAH, 3 sh; Fórnea (SE. of Alcaria), 29S 05170/43789, 2010.05.02, GAH & DTH P43, CGAH, 1 sh; *ca* 1.5 km SE. of Livramento, 29S 05170/43806, 2010.08.06, GAH & DTH P64, CGAH, 64 sh; S. Bartolomeu, 2 km SE. of Nazaré, 29S 04955/43825, 2011.06.04, GAH & DTH P162, CGAH, 1 sh; Ribatejo, SE. of Moitas Venda , 29S 05311/43717, 2010.05.02, GAH & DTH P41, CGAH, 93 sh; Spain, Islas Baleares, Lloc de Monges Vell, Ciutadella, Menorca, 31S EE724228, 2010.08., JQ ex Colln JSTA 11296, CGAH, 1 sh, type locality (QUINTANA, 2010: 154); Prov. Córdoba, 2 km NE. of Cabra, UG4 (37°30´N, 4°25´W), 1984.07.10, DTH, MH & MBS 1984.90.2, NMW.Z.1993.052.10030, 11 sh (9 ad including 7 br); Prov. Málaga, Sierra de San Jorge, Villanueva del Trabuco, 30S UF89, 2001.02, JSTA 6989, CGAH, 4 sh; by N331 *ca* 1 km NW. of Pto. de Las Pedrizas, UF3 (36°59´N, 4°27´W), 1984.07.11, DTH, MH & MBS 1984.92.1, NMW.Z. 1993.052.10048, 1 sh (ad); Sierra de San Jorge, Villanueva del Trabuco, 30S UF89, 2007.09., JSTA 6989, CÁDO, 4 sh; Río Chillar, Nerja, 30S VF2272, 2011.07., JSTA 11591, CJSTA, 7 sh.

T. beckmanni?: Portugal, Beira Litoral, Q. Lágrimas, Coimbra, 29S NE4849, 2010.05.25, ÁDO QDL/09, CÁDO, 2 sh.

***T. callicratis*:** Algeria, by W46 *ca* 2 km SE. of Sidi Yahia, Monts de Tlemcen, 34°43'N, 1°33'W, 1984.07.22, DTH, MH & MBS 1984.175.2, NMW.Z.1993.051.00070, 27 sh (8 ad); by W54 *ca* 2 km S. of Col d'Hafir, Monts de Tlemcen, 34°45'N, 1°26'W,

1984.07.23, DTH, MH & MBS 1984.176.2, NMW.Z.1993.051.00081, 37 sh (16 ad); by W19 12 km SSW. of Oulèd Mimoun, Monts de Tlemcen, 34°48′N, 1°05′W, 1984.07.23, DTH, MH & MBS 1984.179.1, NMW.Z.1993.051.00066, 7 sh (3 ad); by N6 on S. edge of Saïda (S. of Mascara), 34°49′N, 0°09′E, 1984.07.24, DTH, MH & MBS 1984.186.3, NMW.Z.1993.051.00082, 159 sh (33 ad); by N9 *ca* 13 km N. along road from Kherrata (SE. of Bejaïa), 36°34′N, 5°19′E, 1984.08.02, DTH, MH & MBS 1984.256.2, NMW.Z.1993.051.00077, 62 sh (23 ad); by N44 *ca* 1.5 km W. of Bissy (SE. of Skikda), 36°46′N, 7°00′E, 1984.08.03, DTH, MH & MBS 1984.267.1a, NMW.Z.1993.051.00071, 28 sh (11 ad); by W172 11 km WSW. of Kais (E. of Batna), 35°28′N, 6°49′E, 1984.08.06, DTH, MH & MBS 1984.293.2, NMW.Z.1993.051.00084, 46 sh (17 ad); 1 km SE. of N46 at 4 km SW. of Bou-Saada, 35°11′N, 4°09′E, 1984.08.08, DTH, MH & MBS 1984.306.1, NMW.Z.1993.051.00080, 15 sh (4 ad); by W76 8 km S. of El-Hamel (SSW. of Bou-Saada), 35°04′N, 4°06′E, 1984.08.08, DTH, MH & MBS 1984.307.1, NMW.Z.1993.051.00073, 101 sh (25 ad); by N5 *ca* 8 km W. of El Achir (W. of Bordj-Bou-Arréridj), 36°04′N, 4°32′E, 1984.08.09, DTH, MH & MBS 1984.316.1, NMW.Z.1993.051.00068, 31 sh (19 ad); *ca* 2 km E. of N5 at 13 km NW. of Mansoura (WNW. of Bordj-Bou-Arréridj), 36°11′N, 4°25′E, 1984.08.10, DTH, MH & MBS 1984.317.1, NMW.Z.1993.051.00079, 1 sh (ad); Gorges de Beni-Amrane, by N5 6 km NW. of Lakhdaria (SE. of Alger), 36°36′N, 3°58′E, 1984.08.12, DTH, MH & MBS 1984.338.4, NMW.Z.1993.051.00085, 173 sh (>94 ad); by N11 9 km NE. of El-Marsa (WSW. of Ténès), 36°27′N, 0°59′E, 1984.08.14, DTH, MH & MBS 1984.353.1, NMW.Z.1993.051.00065, 1 sh (ad); by N11 5 km SW. of le Guelta (SW. of Ténès), 36°20′N, 0°47′E, 1984.08.14, DTH, MH & MBS 1984.354.1, NMW.Z.1993.051.00069, 14 sh (3 ad); by N11 3.5 km SW. of Khadra (NE. of Mostaganem), 36°14′N, 0°32′E, 1984.08.14, DTH, MH & MBS 1984.357.2, NMW.Z.1993.051.00083, 110 sh (36 ad); by N11 7 km SW. of Khadra (NE. of Mostaganem), 36°13′N, 0°31′E, 1984.08.14, DTH, MH & MBS 1984.358.1, NMW.Z.1993.051.00076, 49 sh (21 ad); by W91A 5 km NNW. of Misserghin (SW. of Oran), 35°39′N, 0°45′W, 1984.08.15, DTH, MH & MBS 1984.367.3, NMW.Z.1993.051.00075, 69 sh (41 ad); by W91A 7 km NW. of Misserghin (SW. of Oran), 35°40′N, 0°46′W, 1984.08.15, DTH, MH & MBS 1984.368.1, NMW.Z.1993.051.00074, 5 sh (1 ad, all old); France, Dept. Ain, 1.5 km NNE. of Pugieu (by road to Virieu-le-Grand), 45°50′N, 5°40′E, 1960.07., MPK (ex DTH 1987.2.1), NMW.Z.1993.052.12899, *ca* 430 sh (>30 ad); Dept. Alpes-Maritimes, Rimiez, N. edge of Nice, 43°43′N, 7°16′E, 1977.12.19, DTH 1977.220a.2, NMW.Z.1993.052.02929, 5 sh (2 ad); Dept. Ariège, Arabaux, 4 km NE. of Foix, 42°59′N, 1°39′E, 1980.08.29, DTH 1981.55.1, NMW.Z.1993.052.04613, 18 sh (9 ad); Dept. Aude, by D118 just N. of Rouffiac-d'Aude, DH1 (43°08′N, 2°18′E), 1984.07.04, DTH, MH & MBS 1984.53.1, NMW.Z.1993.052.09693, 1 sh (ad); Dept. Dordogne, by D48 opposite Font de Gaume, 2 km E. of Les Eyzies, 44°56′N, 1°02′E, 1980.08.21, DTH 1981 13b.7, NMW.Z.1993.052.04325, 25 sh (13 ad); Dept. Drôme, by D93 just SE. of Mirabel-et-Blacons, FK3 (44°42′N, 5°06′E), 1985.08.24, DTH & MBS 1985.368.1, NMW.Z.1993.052.12527, 27 sh (16 ad); Dept. Gard, by D904 4 km SE. of Sauvas, EK4 (44°19′N, 4°10′E), 1983.08.26, DTH & MBS 1983.157.5, NMW.Z.1993.052.08116, 1 sh (ad); Dept. Haute-Savoie, floodline on S. bank of Rhône near Pont Carnot, NE. of Valleiry, 1976.12.26, DTH 1976.229.4, NMW.Z.1993.052.01495, 1 sh (ad old); Dept. Hérault, by D25 2 km E. of St. Pierre-de-la-Fage, EJ1 (43°48′N, 3°27′E), 1983.08.25, DTH & MBS 1983.151.4, NMW.Z.1993.052.08075, 1 sh (ad); Dept. Isère, by D537 2 km NNW. of St.-Disdier, GK1 (44°45′N, 5°53′E), 1985.08.24, DTH & MBS 1985.362.1, NMW.Z.1993.052.12503, 3 sh (ad); Dept. Pyrénées-Orientales, La Preste, 42°24′N, 2°25′E, 1980.09.03, DTH 1981.67.4, NMW.Z.1993.052.04708, 103 sh (53 ad); Great Britain, Dorset, Church Ope Cove, Isle of Portland, UK grid: SY698711, 1977.04.25, RBGW (Ex DTH 1977.150.1), NMW.Z.1993.052.02531, 3 sh (ad); S. of Church Ope Cove, Portland Bill, UK grid: SY696707, 1982.06.14, DTH 1982.138.1, NMW.Z.1993.052.06965, 28 sh (3 ad); Malta, Gozo, Ghar Ilma, S. of Xewkija, 329/860,

2005.03.17, GAH, CGAH, 31 sh; Malta, Ta' Dmejrek, SE. of Dingli, 450/396, 2005.03.18, GAH, CGAH, 12 sh; Morocco, by P24 *ca* 4 km NE. of Zaouïa ech Cheïkh, 32°40'N, 6°52'W, 1984.07.18, DTH, MH & MBS 1984.139.1, NMW.Z.1993.051.00058, >400 sh (68 ad); by P21 *ca* 14 km S. of Timahdite, Moyen Atlas, 33°07'N, 5°01'W, 1984.07.19, DTH, MH & MBS 1984.147.2, NMW.Z.1993.051.00062, 6 sh (ad, old); *ca* 18 km SE. of Sefrou, Moyen Atlas, 33.73°N, 4.70°W, 1984.07.20, DTH, MH & MBS 1984.153.4, NMW.Z.1993.051.00063, >300 sh (47 ad); *ca* 6 km W. of El Menzel, Moyen Atlas, 33°51'N, 4°36'W, 1984.07.20, DTH, MH & MBS 1984.156.6, NMW.Z.1993.051.00060, 64 sh (25 ad); by S5306 *ca* 1.5 km NE. of Taforalt (SW. of Berkane), 34°49'N, 2°24'W, 1984.08.17, DTH, MH & MBS 1984.373.4, NMW.Z.1993.051.00052, 13 sh (3 ad); N. edge of Chechaouèn, 35°10'N, 5°16'W, 1984.08.19, DTH, MH & MBS 1984.386.5, NMW.Z.1993.051.00059, 11 sh (3 ad); E. bank of Oued Ouringa, 2 km SW. of El Jebha, 35°11'N, 4°41'W, 1986.06.28, DTH, MH & MBS 1986.80.4, NMW.Z.1993.051.00047, 20 sh (3 ad); by road 8500 1.5 km due SE. of El-Jebha, 35°11'N, 4°39'W, 1986.06.28, DTH, MH & MBS 1986.81.2, NMW.Z.1993.051.00061, 10 sh (3 ad); by road 5348 14 km SE. along road from Ersaf, 34°06'N, 2°49'W, 1986.06.30, DTH, MH & MBS 1986.101.1, NMW.Z.1993.051.00054, 10 sh (3 ad); by P10 9 km W. along road from Chichaoua, 31°33'N, 8°50'W, 1986.07.08, DTH, MH & MBS 1986.158.1, NMW.Z.1993.051.00050, 1 sh (ad, old); by P10, 10 km WSW. along road from Ounara, 31°30'N, 9°39'W, 1986.07.08, DTH, MH & MBS 1986.162.08 (site 118), NMW.Z.1993.051.00057, 106 sh (14 ad); *ca* 9.5 km SSW. of Essaouira, 31°26'N, 9°47'W, 1986.07.08, DTH, MH & MBS 1986.164.01 (site 120), NMW.Z.1993.051.00049, 48 sh (26 ad); *ca* 9 km NE. along road from Sidi -Kaouki (S. of Essaouira), 31°23'N, 9°45'W, 1986.07.09, DTH, MH & MBS 1986.165.01 (site 121), NMW.Z.1993.051.00048, 13 sh (6 ad); by P8, 2 km SE. of lighthouse at Cap Rhir, 30°37'N, 9°52'W, 1986.07.10, DTH, MH & MBS 1986.176.03 (site 132), NMW.Z.1993.051.00046, 6 sh (4 ad); near P21, 3 km WNW. of El-Hajeb (centre), 33°41'N, 5°25'W, 1986.07.22, DTH, MH & MBS 1986.311.04 (site 267), NMW.Z.1993.051.00055, 22 sh (7 ad); by 5121, 6 km NW. along road from Safi (centre), 32°20'N, 9°15'W, 1986.07.24, DTH, MH & MBS 1986.276.03 (site 232), NMW.Z.1993.051.00045, 1 sh (ad, old); by P3, 6 km ENE. of Sidi-Kacem, 34°14'N, 5°39'W, 1986.07.28, DTH, MH & MBS 1986.306.05 (site 262), NMW.Z.1993.051.00043, 25 sh (5 ad); by old S309, 1.5 km SE. of Zaonïa-d-'Ifrane, 33°33'N, 5°07'W, 1986.07.29, DTH, MH & MBS 1986.313.04 (site 269), NMW.Z.1993.051.00042, 7 sh (5 ad); by track 8 km W. along track from Tounfite, 32°28'N, 5°19'W, 1986.07.31, DTH, MH & MBS 1986.326.1, NMW.Z.1993.051.00044, 46 sh (25 ad); Portugal, Algarve, *ca* 3 km NNW. of Moncarapacho (just S of A22), 29S 060695/410771, 2011.02.04, GAH & DTH P118, CGAH, 59 sh; Beira Litoral, *ca* 0.5 km S. of IC8 at *ca* 2 km WNW. of Ansião, 29S 054642/441843, 2010.09.26, GAH & DTH P75, CGAH, 54 sh; Estremadura, *ca* 1.5 km SE. of Livramento, 29S 05170/43806, 2010.08.06, GAH & DTH P64, CGAH, 37 sh; Ribatejo, Convento de Cristo, just W. of Tomar, 29S 05499/43839, 2011.08.05, GAH & DTH P175, CGAH, 22 sh; Trás-os-Montes, by IP2/N103-7 *ca* 2 km NNE. of Rabal, 29T 06873/46388, 2011.06.29, GAH P170, CGAH, 2 sh; Spain, Prov. Albacete, by N301 3.5 km N. of Cancárix, XH1 (38°26´N, 1°35'W), 1984.07.09, DTH, MH & MBS 1984.78.1, NMW.Z.1993.052.09947, 1 sh (ad); Prov. Almería, El Escaramujo, Alhama de Almería, Sierra de Gádor, 36°57´N 2°34´W, 2009.05., JSTA 10662, CGAH, 3 sh; Prov. Asturias, near N625 in N. part of Desfiladero de los Beyos (by turn to San Ignacio), 30T 033001/478728, 2011.05.13, GAH & DTH E159, CGAH, 49 sh; Prov. Barcelona, Castelldefels, 41°17´N, 1°59´E, undated, JSTA 1799, CGAH, 4 sh; Prov. Cantabria, Desfiladero de la Hermida, by N621 3 km NW. of La Hermida, 43°17´N, 4°38´W, 2001.05.22, GAH, CGAH, 19 sh; Prov. Córdoba, 2 km NE. of Cabra, UG4 (37°30´N, 4°25´W), 1984.07.10, DTH, MH & MBS 1984.90.12, NMW.Z.1993.052.10040, 10 sh (4 ad); Prov. Girona, W. of N152 at Campedevanol (N. of Ripoll), 42°13´N, 2°10´E, 2001.06.16, GAH 2001/37, CGAH, 184 sh; Prov. Granada, Castril, Acequia en Sierra de Castril, 30SWG2085, 2010.05., JSTA, CJSTA 11266; Prov. Logroño, by N111 6 km S. of Torrecillas en

Cameros, 42°12′N, 2°38′W, 1986.06.22, DTH, MH & MBS 1986.50.3, NMW.Z.1993.052.13057, 68 sh (40 ad); Prov. Málaga, Torremolinos, Alrededores arroyo Cueva e la Higuera, Sierra Llana, 30SUF6354, 1991.03., 1992.01. and 1993.12., JSTA, CJSTA 2337; Prov. Murcia, E. slope of Espuña, 30S 062597/419158, 2006.12.16, GAH 2006/03, CGAH, 2 sh; Prov. Tarragona, by N340, 3 km SW. of Hospitalet de l'Infant, CF2, 1984.07.06, DTH, MH & MBS 1984.65.1, NMW.Z.1993.052.09829, 51 sh (31 ad); Prov. Vizcaya, by BI2543 near Dima, 30T 05209/47746, 2011.05.09, GAH & DTH E151, CGAH, 1 sh.

T. callicratis?: Spain, Prov. Girona, by C260 1.5 km W. of Vilafant, DG3, floodline debris from beside River Manol, 115 m, 1983.08.24, DTH & MBS 1983.147.20a, NMW.Z.1993.052.08027, 54 sh (36 ad, 13 imm, 5 very long shells without peristome lip).

T. claustralis: France, Dept. Dordogne, near Grotte des Combarelles just S. of D47 *ca* 2 km E. of Les Eyzies-de-Tayac, 44°57′N, 1°03′E, 2001.06.30, GAH, CGAH, 85 sh.

T. cylindrica: France, Dept. Hautes-Pyrénées, 3 km SE. of St. Marie-de-Campan, 42°58′N, 0°15′E, 1980.08.25, DTH 1981.32.2, NMW.Z.1993.052.04464, 23 sh (13 ad); N. of D923 8.2 km SW. along road from Gavernie, 42°44′N, 0°30′E, 2001.06.28, GAH, CGAH, 20 sh; Dept. Yonne, by N6 at Nailly Saint-Moré, EN3 (47°35′N, 3°47′E), 1983.09.27, DTH & MBS 1983.341.6, NMW.Z. 1993.052.09392, 26 sh, showing some characters of "*T. arcyensis*" (see text); Great Britain, Bedfordshire, Potton, UK grid: 52/229494, 1977.04.07 and 1977.06.06, DTH & RBGW 1977.140.1, NMW.Z.1993.052.02393, 167 sh (20 ad).

T. cylindrica?: France, Corse, 1 km NE. of Tavera, W. of Bocognano, 42°04′N, 9°01′E, 1977.04.15, DTH 1977.96b.1, NMW.Z.1993.052.02063, 1 sh (nearly ad); Dept. Haute-Savoie, N.-facing slope of Salève above Collonges, 46°08′N, 6°10′E, 1976.12.27, DTH 1976.230.5, NMW.Z.1993.052.01508, 61 sh (16 ad); Portugal, Trás-os-Montes, C. Bragança, Bragança, 29T PG8730, 2008.08.16, ÁDO BGÇ/08, CÁDO, 2 sp (*T. cylindrica* or possibly big *T. callicratis*).